

Constraints on Masticatory System Evolution in Anthropoid Primates

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ABSTRACT It is well established that some observed patterns of force production in the primate masticatory system match those predicted by a simplified lever model. This model is also commonly invoked in adaptive explanations of craniodental diversity. However, systematic studies of the predictive power of this model are missing, leaving open the possibility that factors not traditionally included in the model alter the function and evolution of the masticatory system. One such factor was proposed for mammals generally by Greaves ([1978] *J. Zool. (Lond.)* 184:271–285), who argued that the temporomandibular joint (TMJ) was poorly suited to being pulled apart. In this constrained lever model, the avoidance of joint distraction leads to limitations on masticatory system form and function. The goal of the present study was to quantify masticatory system diversity in anthropoid primates for comparison with these predictions.

Results indicate that all sampled taxa exhibit a form that is consistent with selection against regular distraction of the TMJ. Also apparent from observed patterns of scaling is a regular interaction among a limited set of cranial and dental dimensions, in accordance with the constrained model. However, the data indicate that specific positional relationships among the muscles, joints, and teeth differ from those predicted by Greaves (1978). The pattern of deviation suggests that selection has favored a conservative masticatory system configuration that safeguards the TMJ from distraction during the dynamic processing of irregular foods. The resulting buffered model leads to alternative hypotheses regarding the response of the masticatory system to dietary selection pressures. It may, therefore, improve our understanding of the adaptive significance of primate craniofacial form. *Am J Phys Anthropol* 108:483–506, 1999. © 1999 Wiley-Liss, Inc.

Evolutionary changes in the structural relationships within the masticatory system (i.e., among the muscles, joints, and teeth) influence many aspects of facial form in primates. Such changes are commonly viewed as adaptive responses to selection pressures associated with the production of occlusal forces (Du Brul, 1974, 1977; Carlson and van Gerven, 1977; Hylander, 1977, 1979a; Smith, 1978; Ward and Molnar, 1980; Jablonski, 1993; Rak, 1983; Bouvier, 1986;

Ravosa, 1990; Demes and Creel, 1988; Spencer and Demes, 1993; Anapol and Lee, 1994), the resistance to masticatory stresses (Carmill, 1974; Hylander, 1977, 1979a; Rak,

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1983, 1986; Bouvier, 1986; Demes, 1987; Daegling, 1989, 1992), the production of adequate gape (Hylander, 1979a; Smith, 1984; Ravosa, 1990), and the spatial demands of other neurofacial components (Moss and Young, 1960; Cheverud, 1982; Smith and Paquette, 1989; Ravosa, 1991; McCollum, 1994). Since selection may favor opposing adaptive responses, the configuration of the masticatory system is presumed to be a function of the balance among competing and varying demands (e.g., Hylander, 1979a; Smith, 1984; Ravosa, 1990). In this view, limits on diversity simply reflect this balance. However, Greaves (1978, 1982, 1983, 1985, 1988; see also Druzinsky and Greaves, 1979; Werdelin, 1986, 1987, 1988; Spencer and Demes, 1993; Spencer, 1995) proposed a mechanical constraint that could have a consistent limiting influence on masticatory system function and evolution: the temporomandibular joint (TMJ) should not be loaded so that the mandibular condyle is regularly or forcefully pulled away from the articular eminence. The avoidance of such distractive forces is achieved, in Greaves' model, through a combination of 1) changes in masticatory muscle activity by bite point and 2) limitations on the configuration that the masticatory components might assume through evolution. Recently reported electromyographic data from humans are consistent with the first of these expectations (Spencer, 1998) (see below). The goal of the present research is to address the second hypothesis by quantifying the diversity of masticatory system configuration among living anthropoid primates to determine if it appears limited by a restriction on distractive joint loading.

CONSTRAINED MODEL OF MASTICATORY FORCE PRODUCTION

The forces applied to the mandible by the masticatory adductor muscles (i.e., masseter, temporalis, and medial pterygoid) are resisted by reaction forces in three regions of contact with the cranium: the bite point, the working (biting) side TMJ, and the balancing side TMJ (Gysi, 1921; Greaves, 1978; Smith, 1978; Walker, 1978; Wolff, 1984; Hylander, 1985; Spencer, 1998). The relative magnitudes of these forces are determined

largely by their spatial relationships and are commonly examined in the context of a simplified lever model (Weijs and van Spronsen, 1992; Weishample, 1993; Greaves, 1995; Spencer, 1998). Basic predictions derived from this model regarding force production are supported by diverse *in vivo* studies (e.g., Mansour and Reynik, 1975; Hylander and Bays, 1979; Hylander, 1979b; Pruim et al., 1980; van Eijden, et al., 1988). Additionally, it serves as the basis for most adaptive interpretations of masticatory system configuration in relation to dietary selection pressures (e.g., Du Brul, 1977; Hylander, 1977, 1979a; Rak, 1983; Bouvier, 1986; Demes and Creel, 1988; Spencer and Demes, 1993; Anapol and Lee, 1994). The goal of the current study is not to examine the viability of the lever model. Instead, it addresses Greaves' (1978) argument that, within the context of this model, mechanical constraints are at work that limit muscle activity patterns, bite force production, and the evolution of the masticatory system.

In his theoretical treatment of the masticatory system of selenodont artiodactyls, Greaves (1978) presented a general analysis in which masticatory forces are examined in an occlusal view (Fig. 1). As is common among other studies of this system, only the vertical (i.e., perpendicular to the occlusal plane) components of each force are included in the analysis, and they are seen end-on in the occlusal view. Through vector addition, the forces applied by all adductors are combined into a single muscle resultant force. The location of this muscle resultant force is determined by the positions and relative force contributions of the various muscles. When the balancing and working side muscles are equally active (e.g., during maximum force production by both sets of muscles), the muscle resultant force lies in the midline. However, differential activity of the balancing and working side muscles produces mediolateral movement of the muscle force resultant (Hylander, 1985; Throckmorton et al., 1990; Weijs and van Spronsen, 1992; Spencer, 1998).

Because the bite force and joint reaction forces resist the upward pull of the muscles, they lie at the corners of what Greaves (1978) termed the triangle of support (see

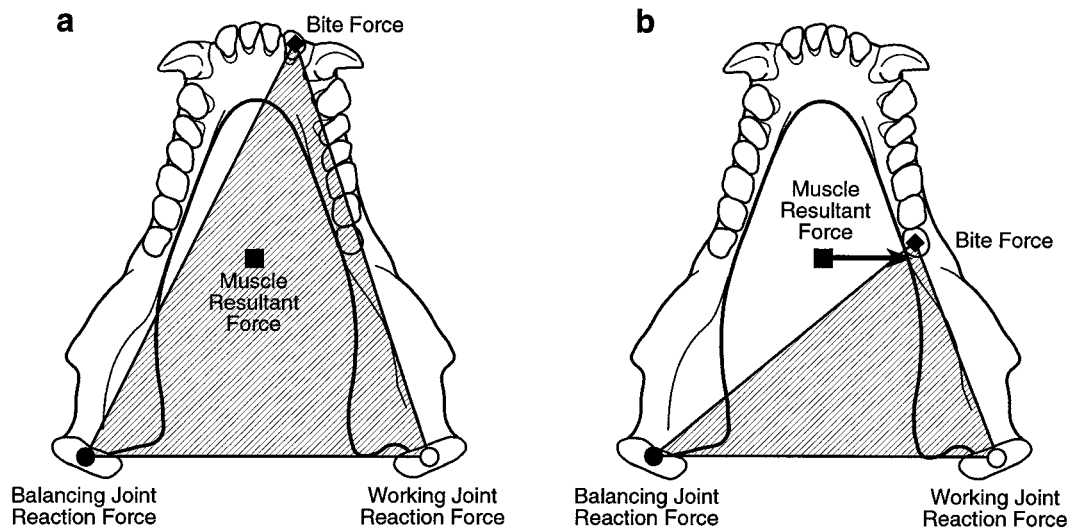


Fig. 1. Occlusal view of mandible showing a vertical midline muscle resultant force (■), which acts to pull the mandible upward out of the plane of the page. During biting at more anterior points (a), this midline muscle resultant force passes through the triangle of support (shaded zone). The corners of this triangle are positioned at the bite force (◆), the balancing side joint

reaction force (●), and the working side joint reaction force (○). Distraction of the working side joint will occur if the muscle resultant force passes outside of the triangle of support (b); Greaves (1978) argued that the muscle resultant would be repositioned toward the working side in such loading situations to avoid tension in the joint.

Fig. 1). The magnitudes of these forces are determined by the position of the muscle force resultant relative to this triangle. During biting at more anterior positions, the triangle of support is relatively large and encloses a midline muscle resultant force (Fig. 1a). Under this loading regime, the forces at the corners of the triangle of support will all be compressive (i.e., they will bring the opposing surfaces together). However, during biting on more posterior teeth, the triangle of support is smaller and shifted toward the working side. A midline muscle resultant force may therefore fall outside the triangle (Fig. 1b), rotating the mandible around the bite point and the balancing side joint so that the working side mandibular condyle is pulled downward (creating a distracting force).

The force patterns described above do not differ from those of other analyses in which both the balancing and working side forces are considered (e.g., Smith, 1978; Walker, 1978; Wolff, 1984; Hylander, 1985). However, Greaves (1978) assumed that the TMJ should not experience the distractive forces that may result during biting on more poste-

rior teeth. He therefore hypothesized that the muscle resultant force moves so that it always falls within the triangle of support, maintaining compressive forces at both joints. In his model, this repositioning is brought about by shifting the muscle force resultant toward the working side through a reduction in the relative activity of the balancing side muscles (Fig 1b).

Changes in joint loading and muscle activity lead to the recognition of three zones of potential bite points that have been termed Regions I, II, and III (Spencer and Demes, 1993; Spencer, 1995, 1998). Regions I and II are separated by an oblique line passing through the balancing side joint reaction force and a midline muscle resultant force (Fig. 2). Bite points anterior to this line in Region I will be associated with triangles of support that enclose a midline muscle resultant force. Movement of the resultant force toward the working side is therefore unnecessary in this region, and there are no limits on maximum muscle forces. Maximum bite force magnitudes in Region I are expected to increase as the bite point is moved posteriorly along the tooth row due to shortening of

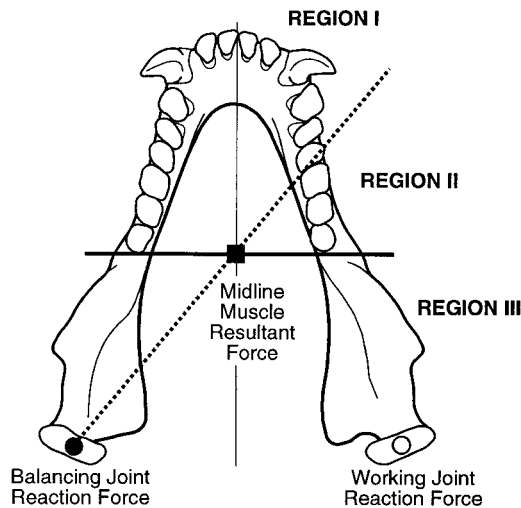


Fig. 2. Occlusal view of mandible showing the predicted distributions of Regions I, II, and III (see text for definitions).

the bite force moment arm. Regions II and III are separated by a transverse line passing through the muscle resultant force (see Fig. 2). Bite points in Region II yield triangles of support through which a midline muscle resultant force will not pass, and this force must shift toward the working side to avoid distraction of the working side TMJ. The decrease in balancing side muscle force that brings about this shift leads to lower maximum bite forces than predicted by an unconstrained model. Furthermore, since the muscle force resultant must shift farther toward the working side as the bite point is moved posteriorly within Region II, the effects on bite forces are more pronounced posteriorly. Maximum magnitude bite forces are therefore predicted to be of relatively high but equal magnitude along that portion of the tooth row that falls within Region II. Bite points posterior to the muscle resultant force will produce triangles of support through which the muscle resultant cannot pass, even through mediolateral repositioning. These bite points lie within Region III, and biting at them will be unavoidably associated with distraction of the TMJ.

Greaves (1978) further speculated that it would be adaptive for specific functional regions of the dentition to maintain consistent positional relationships with the re-

gions defined above. First, Greaves argued that no teeth should lie within Region III (i.e., posterior to the muscle resultant force), since biting on them will lead to joint distraction. Second, he argued that powerful grinding teeth should always be located within what is here termed Region II (i.e., directly anterior to the muscle resultant force), since it is in this region that the highest magnitude bite forces can be produced. Taken together, these predictions require that the muscle resultant force lie immediately posterior to the most distal molar. Furthermore, it is expected that the position and mesiodistal length of the powerful grinding dentition will be correlated with the distribution of Region II.

PATTERNS OF COVARIATION IN THE CONSTRAINED MODEL

Three parameters interact to determine the distribution of Region II and its relationship to the dentition in Greaves' model (Spencer and Demes, 1993; Spencer, 1995, 1998): 1) the distance of the balancing side joint reaction force from the midline, 2) the distance anterior to the TMJ of the point of intersection of the muscle resultant force with the occlusal plane, and 3) the mediolateral position of the tooth row. First, evolutionary changes in the mediolateral position of the balancing side TMJ leads to a reorientation of the line demarcating Regions I and II (Fig. 3a), altering the anterior border of Region II. If Greaves' (1978) constrained model is correct, therefore, lateral movement of the TMJ should be accompanied by an evolutionary reduction in the mesiodistal length of the dentition (and vice versa). Second, both boundaries defining Regions I, II, and III pass through the midline muscle resultant force and are repositioned with anteroposterior movements of the resultant (Fig. 3b). Posterior muscle resultant force migration is associated with both a posterior migration of Region II and a change in its shape. The molar dentition should adapt by migrating posteriorly and decreasing in mesiodistal length (either by changes in tooth size or by the elimination of teeth from the molar-like functional unit.) Finally, Region II tapers medially, and its anteroposterior length is therefore shorter close to the mid-

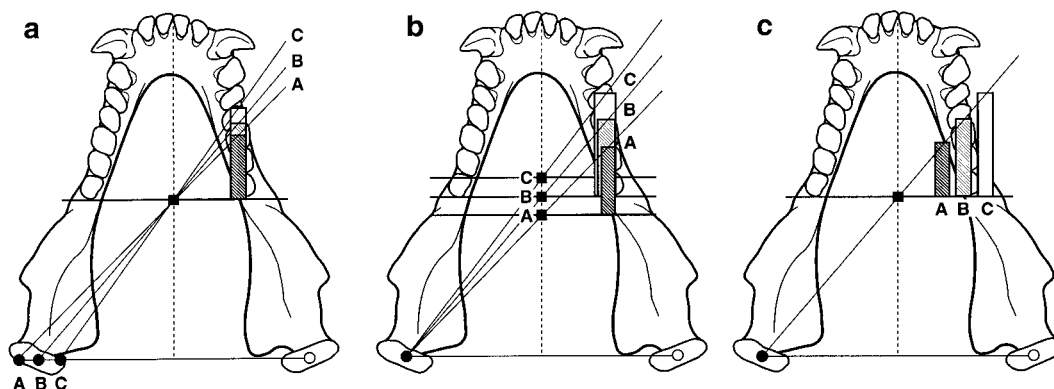


Fig. 3. Diagrams showing the effects of changes (represented by states A, B, and C) in the relative positions of the muscle and joint forces on the distribution of Region II. **a:** Mediolateral movement of the balancing side joint force (●) leads to a reorientation of the boundary between Regions I and II (diagonal line) so that more or less of the tooth row (shaded boxes) falls within Region II. **b:** Anterior movement of the midline

muscle resultant force (■) causes Region II to be positioned more anteriorly; its anteroposterior length (at a given mediolateral position) will also increase. **c:** Because Region II tapers medially, its anteroposterior length is shorter near the midline, and it should accommodate fewer (or shorter) molar-like teeth.

line. A more medially positioned tooth row should therefore be shorter than a more laterally positioned tooth row, all other parameters being equal (Fig. 3c).

The primate masticatory system differs from the model of Greaves (1978) in that the TMJs are usually positioned above the occlusal plane and the muscle resultant vector is probably rarely perpendicular to this plane. These parameters together can act to expand Region II by reorienting its boundary with Region I. They do so by altering the positional relationship of the muscle resultant vector to the triangle of support. Because the bite point forms one corner of the triangle of support, raising the other corners of the triangle (those at the balancing and working side TMJs) above the occlusal plane causes the triangle of support to become inclined (Fig. 4). This reorientation separates the point where the muscle resultant force vector intersects the occlusal plane (point A in Fig. 4) from its intersection with the triangle of support (point B in Fig. 4). In Greaves' model, these points are always coincident. However, when separated they are independent; a reorientation of the resultant force vector can alter where it passes relative to the triangle of support without affecting where it pierces the occlusal plane. Therefore, a muscle resultant that appears

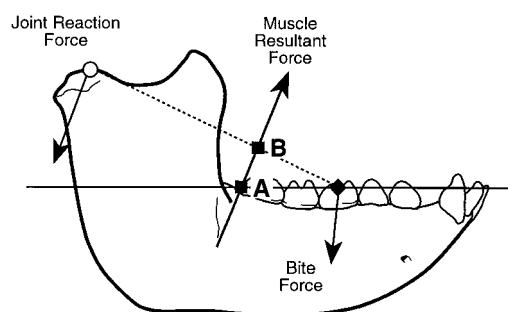


Fig. 4. Lateral view of mandible illustrating the effects of positioning the TMJ above the occlusal plane and inclining the muscle resultant force. In this configuration, which is common among primates, the muscle resultant intersects the triangle of support (seen edge on as a dashed line) more anteriorly (B) than its intersection with the occlusal plane (A). As a result, a muscle resultant force that appears to pass through the triangle of support in the occlusal view might actually lie anterior to it. This will influence the distribution of Region II.

to pass through the triangle of support in Greaves' occlusal view model might actually pass anterior to the triangle if its vector were inclined anterosuperiorly. Since such a force vector no longer passes through the triangle of support, it must be shifted toward the working side to avoid joint distraction, in compliance with Greaves' constraints. Bite points that were not in Region II accord-

ing to Greaves' predictions will therefore lie within Region II in this modified model. This anterior extension of Region II along the tooth row is proportional to the combined degree of muscle inclination and TMJ height; if the muscle resultant force is vertical or the TMJs lie within the occlusal plane, no anterior expansion will occur (for further discussion see Spencer, 1995).

APPLICABILITY OF CONSTRAINED MODEL TO PRIMATES

The fundamental assumption of the constrained model is that the TMJ is poorly structured for resisting distractive forces. In primates, it is likely that the TMJ can withstand such forces, at least at low to moderate magnitudes. Based on patterns of subcondylar bone strain in a macaque, Hylander (1979b) inferred the existence of intermittent distractive forces in the working side TMJ during unilateral isometric biting on the third molar. Distractive forces would presumably be resisted by tension in the temporomandibular ligament (Hylander, 1979b). However, the ability of this ligament to resist gross dislocation of the TMJ does not imply that it regularly serves to maintain joint congruity during function. To the contrary, the structure of this ligament suggests that it acts to limit extremes of motion (particularly in the posterior direction) but that it cannot hold the mandibular condyle against the articular eminence in normal loading positions (Bell, 1990). Given the importance of joint stability to the guidance of tooth contacts (Bakke and Møller, 1992), it seems unrealistic to suppose that repetitive separation of the condyle from the articular eminence occurs during routine mastication. In support of this, Hylander (1979b) inferred only compressive joint reaction forces during mastication in several macaques. Furthermore, clinical studies in humans suggest that injury to this ligament or the structurally contiguous joint capsule can permanently impair normal joint function (Bell, 1983, 1990; McKay, 1992). Given the fundamental role of this joint in food processing, selection against morphologies that increase the chances of such injuries is likely to be high.

Additional experimental data relevant to testing the predictions of the constrained model are few. Because these predictions are formulated for maximum force production, any experimental test must involve recording forces during heavy unilateral loading at several known bite points. Few studies have met these requirements. For example, while the distinctive pattern of maximum magnitude bite forces predicted by the constrained model should be quantifiable, few studies report data from multiple bite points along the tooth row, and none report data for all postcanine teeth. Furthermore, the available studies differ in their conclusions, with maximum voluntary bite forces in humans having been reported to increase posteriorly at the rate predicted by the unconstrained models (van Eijden et al., 1988; van Eijden, 1991), increase posteriorly but more slowly than expected (Mansour and Reynik, 1975), and decrease posteriorly (Pruim et al., 1980).

A more direct method of testing the constrained model would be to compare relative balancing and working side muscle activity during maximum bite force production at points along the tooth row. As discussed above, this model requires that, during high magnitude biting, the activity of the balancing side muscles will decrease relative to that of the working side muscles as the bite point is shifted posteriorly along the molar dentition. Recent electromyographic work in humans (Spencer, 1998) supports this central prediction. This pattern of activity was recorded from the superficial masseter and the anterior temporalis muscles of nine human subjects. These data are difficult to interpret outside of the context of the constraints proposed by Greaves (1978) and offer indirect support for the hypothesis that distraction of the TMJ is to be avoided.

The goal of the present study is to determine if the observed position and dimensions of the postcanine dentition covary with the distribution of Region II (the zone of highest magnitude bite force production), as predicted by the constrained model described above. If the model has been influential during the evolution of anthropoid primates, masticatory form in this group should be limited in accordance with its predic-

TABLE 1. Taxa included in study

Taxon	M	F	Taxon	M	F
<i>Aotus azarae</i>	5	5	<i>Macaca fascicularis</i>	15	15
<i>Callicebus torquatus</i>	15	15	<i>Macaca arctoides</i>	12	10
<i>Callicebus moloch</i>	15	15	<i>Cercocebus albigena</i>	15	15
<i>Alouatta seniculus</i>	15	15	<i>Cercocebus torquatus</i>	15	11
<i>Alouatta palliata</i>	15	15	<i>Cercopithecus nictitans</i>	15	15
<i>Lagothrix lagothricha</i>	5	5	<i>Cercopithecus cephus</i>	15	15
<i>Ateles geoffroyi</i>	5	5	<i>Erythrocebus patas</i>	14	5
<i>Brachyteles arachnoides</i>	2	1	<i>Papio anubis</i>	15	15
<i>Saguinus oedipus</i>	15	15	<i>Mandrillus sphinx</i>	8	3
<i>Leontopithecus rosalia</i>	1	1	<i>Theropithecus gelada</i>	13	3
<i>Callithrix jacchus</i>	12	14	<i>Colobus guerza</i>	15	15
<i>Cebuella pygmaea</i>	12	2	<i>Colobus polykomos</i>	15	15
<i>Cebus apella</i>	15	15	<i>Presbytis cristatus</i>	5	5
<i>Cebus albifrons</i>	15	15	<i>Nasalis larvatus</i>	5	5
<i>Saimiri sciureus</i>	5	5	<i>Simias concolor</i>	5	5
<i>Pithecia pithecia</i>	15	13	<i>Pygathrix nemaeus</i>	5	5
<i>Chiropotes satanas</i>	15	15	<i>Hylobates hoolock</i>	5	5
<i>Cacajao melanocephalus</i>	13	8	<i>Pan troglodytes</i>	15	15
<i>Cacajao calvus</i>	12	15	<i>Gorilla gorilla</i>	15	8
			<i>Homo sapiens</i>	46	22

tions.¹ If conformity to this limitation were observed in all anthropoid taxa, it would suggest that either the predictions of the constrained model are correct or that evolution has simply not produced a form that is incompatible with the model (an unlikely occurrence, given the broad phenotypic range of anthropoid taxa). If observed diversity is not so limited, the model must be rejected or modified.

MATERIALS AND METHODS

Sample

Representative species of most extant anthropoid genera were included in this study (Table 1) to increase the probability of sampling a taxon that is incompatible with the constrained model. A total of 876 individuals was measured representing 39 species and 31 of the 37 anthropoid genera recognized by Fleagle (1988). Only adult crania (maxillary canine fully erupted) and their associated mandibles were used. Specimens were obtained from the following sources: the American Museum of Natural History (New York, NY), the National Museum of Natural History (Washington, DC), the Field Museum of Natural History (Chicago, IL), the Museum

of Comparative Zoology (Cambridge, MA), and the British Museum of Natural History (London). No material from captive animals was used.

Measurements

Three sets of measurements were recorded from the above sample: 1) distances that represent the observed position and mesiodistal length of the postcanine dentition, 2) the dimensions needed to calculate a predicted position and length of the postcanine dentition using the described model, and 3) estimates of the positions and orientations of the primary masticatory adductor muscles. Both three-dimensional (3-D) coordinate data and 2-D linear and angular data were quantified using MacMorph© (Spencer and Spencer, 1993), a computer-driven video-image analysis package for the Apple Macintosh computer. Details of the 3-D data collection method can be found in Spencer and Spencer (1995).

The landmarks for which 3-D coordinate data were collected are shown in Figure 5. These data formed the basis for the calculation of most dimensions used in this study. Five dimensions together determine the distribution of Region II: 1) the distance of the balancing side joint reaction force from the midline, 2) the distance of the working side postcanine tooth row from the midline, 3) the height of the TMJ above the occlusal

¹Prosimian primates were not included in this study because, unlike anthropoids, all extant taxa possess an unfused mandibular symphysis, a feature that is thought to change the way working and balancing side forces are produced (Beecher, 1977, 1979; Hylander, 1979a, 1984; Greaves, 1988; Ravosa, 1991).

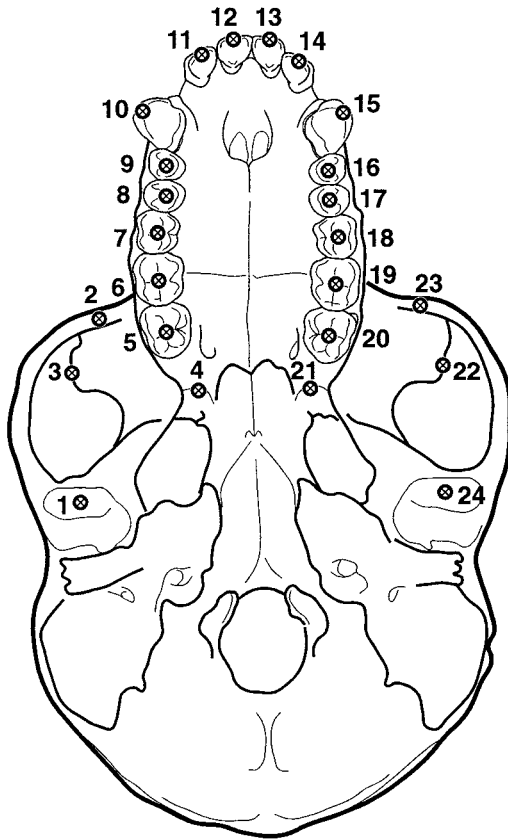


Fig. 5. Landmarks for which three-dimensional coordinate data were collected. 1,24, center of articular surface of articular eminence; 2,23, inferior edge of malar at most anterior point of attachment of superficial masseter muscle; 3,22, point of intersection of temporal line and frontozygomatic suture (frontomalare temporale [White, 1991]); 4,21, sphenopalatine suture at intersection of medial and lateral pterygoid plates; 5–9 and 20–16, the center of the trigon basins of each maxillary molar and premolar; 10,15, maxillary canine tip; 11–14, center of occlusal surface of each maxillary incisor.

plane, 4) the distance anterior to the TMJ that a midline muscle resultant force intersects the occlusal plane, and 5) the orientation of a midline muscle resultant force in the sagittal plane. Of these, the first three could be directly quantified from the 3-D landmark data (see Appendix). However, quantifying muscle resultant position and orientation is severely hampered by our poor knowledge of the comparative myology and function of the masticatory adductor musculature among primates (Throckmorton, 1985, 1989). It was therefore assumed

that the maximum magnitude muscle resultant force crosses the occlusal plane at a point in the midline directly at the posterior end of the tooth row. This position corresponds to that hypothesized by Greaves (1978) and therefore provides a directly quantifiable value that is consistent with the assumptions of the constrained model. As such, it should be regarded as a liberal estimate since the model is viewed as being correct with regard to resultant position.

The accuracy of the assumed muscle resultant force position was tested by comparing it to estimated masticatory muscle force vectors. Although the combination of individual forces into a resultant vector is problematic, the possible locations of this resultant can be bracketed by examining the separate positions of the component forces. Each muscle force vector intersects the occlusal plane at some position anterior to the TMJ. Since the resultant of two (or more) of these vectors is intermediate in orientation, it must cross the occlusal plane between their separate points of intersection. The points where the estimated force vectors for the anterior temporalis, superficial masseter, and medial pterygoid muscles intersect the occlusal plane were therefore quantified and compared to the position of the muscle resultant force assumed in the constrained model.² Approximate centroids of the attachment areas for all muscles were first marked on each specimen. Lateral view images of each specimen were then displayed within MacMorph, and the marked cranial and mandibular centroids were connected as an estimate of the force vector for each muscle. The points where each "vector" intersected the occlusal plane were then measured for comparison to the assumed intersection point.

Muscle resultant orientation could not be reliably estimated from the data collected for this study since this value is dependent on unknown muscle force magnitudes. Sample means for the quantified orientation of estimated muscle force vectors are as follows

²The constrained model of Greaves (1978) assumes static equilibrium, a scenario that is most similar to isometric biting. The deep masseter and posterior temporalis muscles were therefore excluded from the present analysis because they are thought to contribute only a weak force during isometric biting (Ahlgren, 1966; Møller, 1966; Hylander and Johnson, 1994).

(90° = perpendicular to the occlusal plane (in the sagittal plane), <90° = inclined anteriorly): anterior temporalis, $91.90 \pm 6.9^\circ$; superficial masseter, $77.5 \pm 6.5^\circ$; medial pterygoid, $81.2 \pm 8.0^\circ$. Based on these values, a fixed orientation of 80° was assumed for all taxa in this study. This value allows variation in the height of the TMJ above the occlusal plane to have only a moderate influence on the calculation of Region II distribution (see above).

The five parameters described above were used to calculate the length of the tooth row that should fall within Region II. This predicted length will be referred to as the effective length of Region II. The procedure by which this length was calculated is provided in the Appendix.

Test criteria

Greaves (1978) proposed the constrained model for application to selenodont artiodactyls, in which the grinding tooth row is easily identified due to the morphological similarity of the teeth of which it is composed. However, the diversity of premolar form among anthropoid primate species suggests these teeth experience varied loading patterns (Rosenberger, 1992). Therefore, it may be selectively advantageous for some taxa to include the premolars within Region II, but it is difficult to predict *a priori* which taxa should do so. However, the most basic predictions of Greaves' (1978:276–277) model with regard to expected tooth position are that "regardless of the muscle resultant's position, powerful grinding teeth are not expected either posterior to the most posterior position of the muscle resultant or anterior to the region of maximum force application [Region II in the present work] where tooth force rapidly decreases."

These requirements give rise to two predictions tested here. First, the effective length of Region II should be equal to or greater than the observed distance between the trigon basins of the anterior- and posterior-most molar teeth. If observed molar row length were found to exceed the effective length of Region II in any taxa, it would imply that a tooth need not lie in Region II to function effectively as a molar. Second, the estimated position of Region II should corre-

spond to that predicted by the model. This is tested by comparing the muscle resultant force position assumed in the model to the observed points of intersection between individual muscle force vectors and the occlusal plane. If the assumed resultant force is not bracketed by the estimated muscle vectors in all taxa, it implies that the muscle resultant cannot be positioned as predicted during isometric loading. Failure of this test would suggest either that some teeth fall posterior to Region II, where it is expected that loading the teeth would produce tensile forces in the working side joint or that some portion of Region II is not occupied by teeth even though it is well suited for the application of loads to molars.

Statistical procedures

The predictions described above were evaluated through examination of plots of predicted and observed dimensions. For comparison of the observed and predicted values, it was useful to standardize the data so that differences between taxa due to size were reduced. In most instances the relative size of a limited set of variables was the subject of interest, and the data were standardized against some parameter that makes the plot easier to interpret. This approach is not meant to imply that the chosen standardizing variables are indicative of overall size; they are used merely as indications of local size.

Broad patterns of scaling among the dimensions that influence the distribution of Region II were examined as a way to explore their potential interaction across anthropoids. Based on model predictions regarding covariation among these dimensions, it is expected that allometric change in one parameter (i.e., change in shape with size) will be accompanied by compensatory allometric changes in other parameters so that the effective length of Region II scales with postcanine dimensions. For the purpose of comparing dimensions to overall facial size, a geometric mean (Darroch and Mosimann, 1985) of five dimensions was calculated (these dimensions were calculated using the 3-D coordinate data set and include biarticular breadth (landmark 1 to landmark 24), palate breadth (landmark 7 to landmark

18), temporal foramen length (landmark 1 to landmark 2), tooth row length (landmark 20 to landmark 16) and infratemporal height [landmark 4 to landmark 3]). Scaling relationships were established by logging the data and regressing dimensions indicative of shape on the geometric mean. Examination of the slope of a regression line in log space allows inferences to be made regarding the scaling of variables, and, when an estimate of size is used, this approach provides an indication of shape changes associated with size (Mosimann and James, 1979). To test if an observed slope differed significantly from isometry (no change in shape with size), 95% confidence limits for the slope of the reduced major axis (RMA) regression line were calculated in NEWRMA (Cole, 1997) and compared to a slope of 1.0. Slopes for separate regression lines were compared using the Clarke (1980) test, and, when they were found to be parallel, elevations were compared using a modification of Tsutakawa and Hewitt's (1977) quick test. These tests were performed in NEWRMA.

RESULTS

Region II distribution

Figure 6 compares the predicted effective length of Region II to actual postcanine tooth row dimensions. In this figure, three distances are shown: 1) the observed distance (measured between the trigon basins) separating the most mesial premolar and the most distal molar, 2) the observed distance between the first and last molars, and 3) the calculated effective length of Region II. All values are scaled to the distance between the first and last molars. The shaded zone between 0.0 and 1.0 therefore represents the molar dentition, with M^1 positioned at 1.0 for all specimens and the most distal molar positioned at 0.0. The positions, in relation to the molar dentition, of the most anterior premolar and the anterior end of Region II are indicated by box plots; Region II is therefore predicted to extend from 0.0 to this anterior position.

The data in Figure 6 show systematic differences in the relative lengths of the molar and premolar dentition between groups that differ in postcanine dental for-

mula. However, within groups with the same dental formula, the relationship between premolar row length and molar row length is generally consistent. Additionally, this relationship is maintained despite differences in body size; taxa with very different body weights (e.g., *Aotus azarae* (800 g) and *Alouatta palliata* (5,700–8,000 g) [Ford and Davis, 1992]) show a similar length of their premolar tooth rows relative to their molar rows.

The anterior border of Region II was consistently predicted to intersect the tooth row in the premolar region (see Fig. 6). Therefore, when the muscle resultant force position assumed by Greaves (1978) is used, Region II envelopes the entire molar dentition and some portion of the premolar dentition in all taxa. Additionally, Region II does not extend anterior to the most mesial premolar in any taxa, though it does closely approach this position in the Callitrichids and in *Mandrillus*. With the exception of these few taxa, therefore, the effective length of Region II appears to maintain a reasonably uniform relationship with observed tooth row dimensions within broad taxonomic groups. As anticipated, there is variation within more restricted groupings that does not always match that seen in either molar row length or total postcanine tooth row length. For example, the effective length of Region II differs between *Alouatta seniculus* and *Alouatta palliata* even though these taxa differ little in relative premolar row length.

The above results suggest that the parameters that influence the distribution of Region II covary among anthropoid primates so that, minimally, all molar teeth are maintained within this region. Not demonstrated in these plots is the range of variation in these parameters within this group. Were they found to differ widely among taxa, the observation that Region II envelopes a consistent portion of the tooth row would assume greater significance. A casual consideration of the cranial form of some of the included taxa makes it clear that the determinants of the distribution of Region II do differ substantially across anthropoids (e.g., *Cebus*, *Alouatta*, *Papio*, *Gorilla*, and *Homo*). A quan-

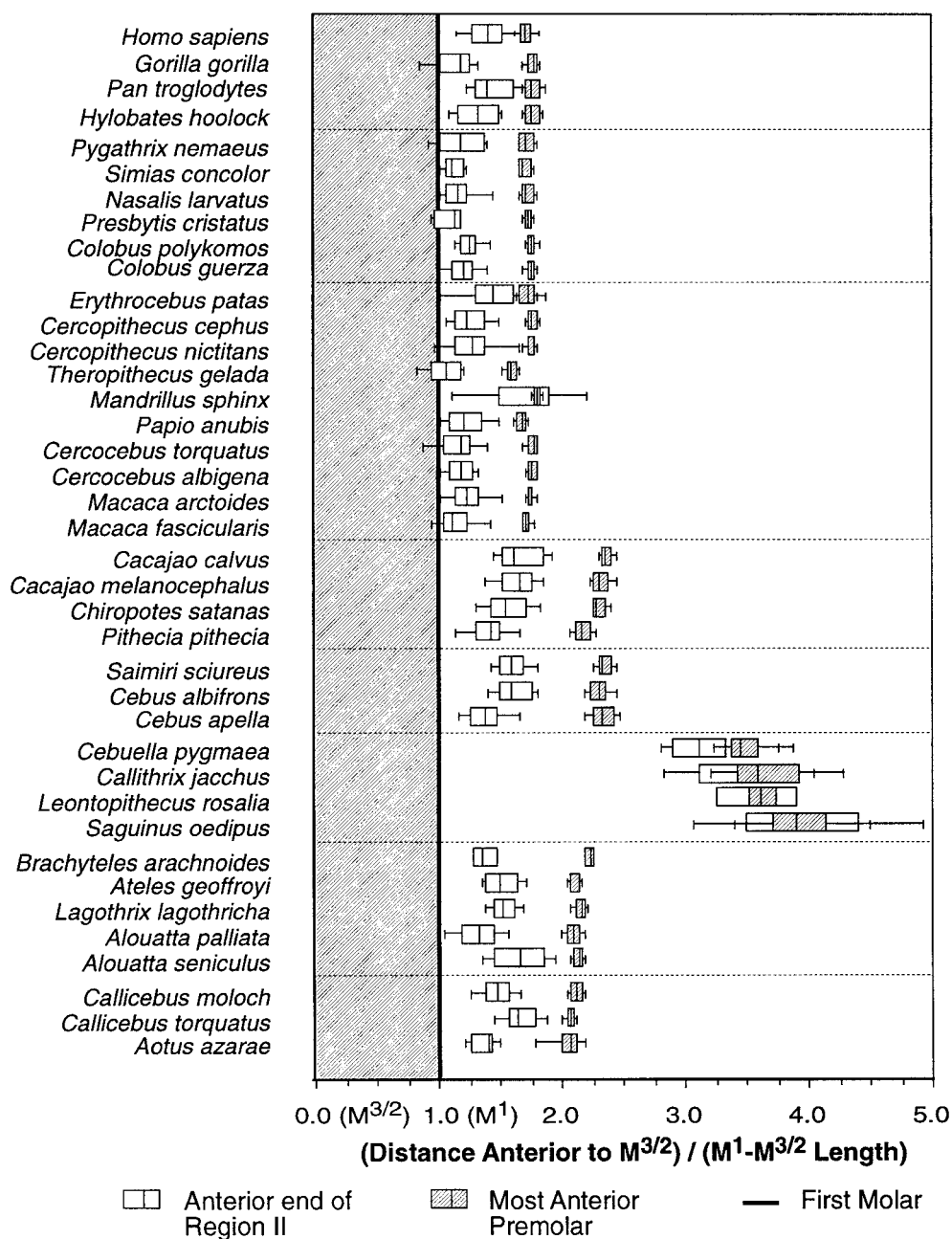


Fig. 6. Plot comparing quantified postcanine dimensions to effective Region II length (as calculated using a muscle resultant force positioned at the posterior end of the tooth row). All values are standardized against $M^1 - M^{3/2}$ intertrigon distance. M^1 therefore lies at a value of 1.0 (bold line), and the molar dentition fills the

distance between 0.0 and 1.0 (shaded zone) in all taxa. Variation in the position of the most anterior premolar and the predicted anterior edge of Region II is represented by a box plot. The box encloses the central 50% of the data, the horizontal bar encloses the central 80% of the data, and the vertical bar indicates the median.

TABLE 2. Reduced major axis regression parameters for sex-specific mean values of each dimension plotted against the geometric mean¹

Dimension	Taxon	R ²	Y-intercept	RMA slope	Lower confidence limit	Upper confidence limit
Molar row length	1) Catarrhines	0.904	-1.097	1.051	0.913	1.211
	2) Noncallitrichid platyrrhines	0.941	-1.958	1.250	1.097	1.424
	3) Callitrichids	0.890	-1.761	0.974	0.627	1.513
<i>Slope comparison</i> ²	1 = 2 = 3 = 1					
<i>Intercept comparison</i> ³	1 >> 2 >> 3 << 1					
Postcanine length	1) Catarrhines	0.918	-0.460	1.029	0.903	1.173
	2) Noncallitrichid platyrrhines	0.974	-1.036	1.209	1.108	1.319
	3) Callitrichids	0.976	-0.749	1.084	0.874	1.344
<i>Slope comparison</i> ²	1 < 2 = 3 = 1					
<i>Intercept comparison</i> ³	1 ⁴ 2 = 3 < 1					
Effective region II length	1) Catarrhines	0.922	-1.412	1.192	1.049	1.355
	2) Noncallitrichid platyrrhines	0.951	-1.496	1.235	1.096	1.392
	3) Callitrichids	0.991	-1.129	1.220	1.067	1.395
<i>Slope comparison</i> ²	1 = 2 = 3 = 1					
<i>Intercept comparison</i> ³	1 = 2 << 3 >> 1					
Biarticular breadth	All	0.993	0.573	0.951	0.926	0.977
Palate breadth	All	0.991	0.193	0.896	0.869	0.923
Muscle resultant AP position	All	0.972	-0.332	1.035	0.981	1.092
Glenoid height	All	0.919	-4.200	1.932	1.766	2.113

¹ =, no significant difference; >, significant at $P < 0.05$; >>, significant at $P < 0.01$; *no test for elevation performed due to significantly different slopes.

² Results of tests for differences in slope using NEWRMA (Cole, 1997). Numbers correspond to listed taxa.

³ Results of tests for differences in elevation using NEWRMA (Cole, 1997). Numbers correspond to listed taxa.

⁴ No test for elevation performed due to significantly different slopes.

titative way of exploring this issue is to examine how each configurational parameter changes with size.

Table 2 summarizes the RMA regression parameters for bivariate log-log plots of sex-specific mean values for the relevant variables regressed on the geometric mean. Included are data showing how postcanine mesiodistal dimensions (measured between the trigon basins of maxillary teeth) scale with masticatory system size. Because it is evident in Figure 6 that relative molar/premolar dimensions vary among groups with different dental formulae, separate regression lines are calculated for catarrhines, three-molared platyrrhines, and two-molared callitrichids. Despite differences in molar proportions among groups (as evidenced by significantly different intercept values among the groups), overall postcanine tooth row length scales isometrically relative to facial size and appears roughly similar in all anthropoids, with one exception: the length of the postcanine dentition scales with slight positive allometry in non-callitrichid platyrrhines. This pattern corre-

sponds to previously reported dental dimensions and probably relates to the strong trend toward greater folivory with increasing body size in platyrrhines (Kay and Hylander, 1978). When the scaling of the effective length of Region II is compared to that found for postcanine tooth row length and molar row length, no significant differences in slope are found in any of the three examined groups; the effective length of Region II scales at a rate comparable to postcanine tooth row length.

Roughly isometric scaling of the effective length of Region II could result from shape maintenance across all sizes in the parameters that influence this length. However, the data in Table 2 indicate that several of the dimensions used to predict the effective length of Region II scale allometrically with masticatory system size. Both palate breadth and biarticular breadth scale with negative allometry, while glenoid height scales with strong positive allometry. As discussed above, the theoretical effect of reducing palate breadth is to shorten the calculated effective length of Region II. Were palate breadth the

only parameter to scale allometrically with size, the effective length of Region II should also scale with negative allometry. However, the size-related shape changes in biarticular breadth and glenoid height are predicted to lead to an increase in the effective length of Region II. Thus, these additional trends moderate the influence of changing palate breadth with the result that the effective length of Region II scales in concert with observed tooth row dimensions.

Test of assumed muscle resultant force position

The data presented in the preceding section regarding the effective length of Region II were based on the assumption that the resultant force of all jaw adductor muscles crosses the occlusal plane directly posterior to the tooth row (as proposed by Greaves [1978]). This assumption was tested by comparing this muscle resultant position to estimates of individual muscle force vector positions. The point where each muscle force vector intersects the occlusal plane was measured as a distance anterior to the articular eminence within the occlusal plane. The resulting values are shown in Figure 7 for the superficial masseter, anterior temporalis, and medial pterygoid muscles. In this figure, the point where each muscle vector intersects the occlusal plane is shown in relation to the anteroposterior (A-P) positions of the TMJ and most distal molar. All values are standardized so that the articular eminence lies at 0.0 on the horizontal axis and the distal molar lies at 1.0. This method of standardization allows for easy comparison of muscle force vector/occlusal plane intersection points to the assumed muscle resultant position, which lies in the same A-P position as the distal molar (i.e., at a value of 1.0).

Examination of Figure 7 shows that none of the three muscle force vectors intersects the occlusal plane at a point anterior to the most distal molar. While these intersection points do vary, the position of the intersection point for each muscle vector is visually quite consistent across all taxa. On average, the anterior temporalis vector intersects the occlusal plane most anteriorly (mean standardized A-P distance = 0.66 ± 0.15 stan-

dard deviation). The medial pterygoid force vector intersects the occlusal plane most posteriorly (mean standardized A-P distance = 0.40 ± 0.08). The superficial masseter intersection point lies between those of the other two muscles (mean standardized A-P distance = 0.57 ± 0.09). The relatively low values for all taxa suggest that in anthropoids the resultant of the three force vectors that are active during isometric biting does not intersect the occlusal plane near the distal molar, as assumed by Greaves (1978) for selenodont artiodactyls.

DISCUSSION

The configuration of the masticatory system in anthropoid primates has responded to a variety of selection pressures during the evolutionary diversification of this group. A fundamental issue explored in this study is whether this configuration is influenced primarily by the equilibrium reached among selection pressures that vary among species or if it also is constrained by a universal need to avoid distraction of the temporomandibular joint, as proposed by Greaves (1978). The distinction made between these possibilities does not imply that a constraint on joint loading stems from some process independent of selection; it is selection, acting to favor individuals that do not distract their TMJ, that is expected to produce gaps in the set of observed phenotypes (for a discussion of the overlap between the concepts of constraint and selection see Smith, 1993; Schwenk, 1995). Instead, the distinction lies between those selection pressures whose strength is governed by varying aspects of behavior (such as gape or diet) and one that is thought to be invariable among species.

The results of the broad-scale morphometric analysis reported here suggest that phenotypic diversity in cranial form within anthropoids is limited by the need to avoid distraction of the TMJ. Furthermore, this diversity conforms to several basic predictions of a modified version of Greaves' (1978) constrained model (which includes numerous secondary elements beyond the basic limit on joint loading); patterns predicted by the model are evident throughout this group. However, it is also apparent that there is an important incongruity between observed

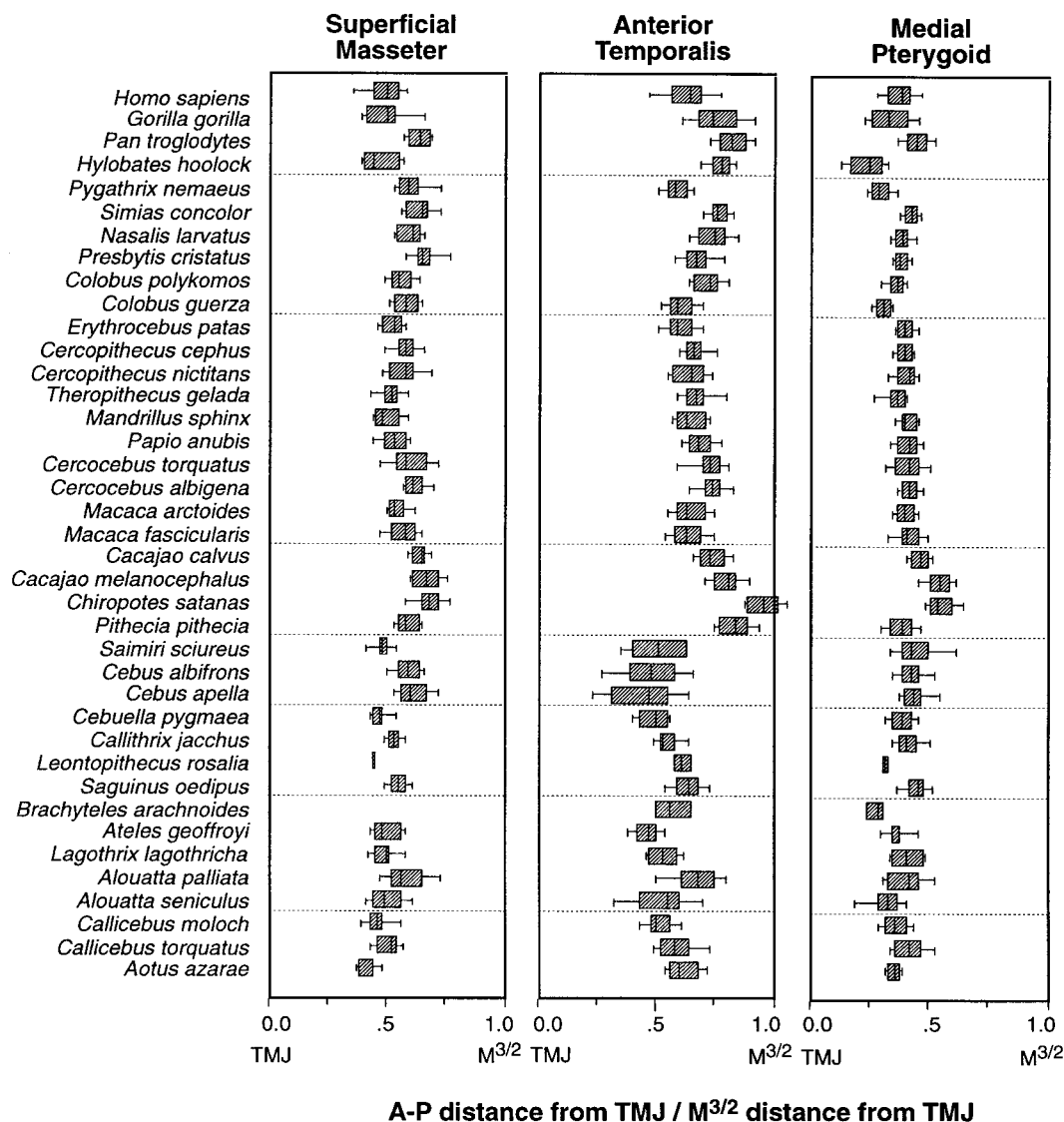


Fig. 7. Three graphs showing the relative positions of the points where estimated force vectors intersect the occlusal plane. Intersection points are shown in relation to the TMJ and most distal molar, with all values scaled to the distance of the distal molar anterior to the TMJ. The posterior end of the tooth row therefore lies at a value of 1.0 in all taxa. This figure indicates that the force vectors for the primary jaw adductors all lie well posterior to the end of the tooth row. See Fig. 6 for box plot definitions.

morphology and this modified model. This discrepancy lies in the observation that the masticatory adductor muscles are not positioned to produce a resultant force directly at the posterior end of the tooth row during forceful isometric biting. Instead, in all of the examined taxa they are positioned more posteriorly (on average, approximately 60%

of the distance from the TMJ to the posterior molar). Greaves (1978) argued that all molar-like teeth should lie directly anterior to the muscle resultant force within the specific region where the highest forces can be produced, here termed Region II. However, the relatively posterior positioning of the primary jaw adductors found in anthropoids

suggests that natural selection has failed to take advantage of this seemingly more optimal region of bite force production.

Two lines of evidence, however, suggest that the molar dentition of primates does in fact lie within Region II and responds to changes in the distribution of this region. The data presented above indicate that the test criterion requiring all molars to lie within Region II is uniformly complied with when it is assumed that the muscle resultant force crosses the occlusal plane directly posterior to the tooth row. Indeed, the portion of the tooth row located in Region II is quite consistent, especially among taxa with similar dental formulae. These observations hold despite the wide range of cranial configurations found among anthropoid primate taxa. Much of this variation is reflected in the interspecific scaling relationships among the parameters that influence effective Region II length. The data reported in Table 2 indicate that most of these parameters exhibit an allometric relationship with cranial size; the configuration of the masticatory system changes with size. Despite such overall trends, the portion of the tooth row predicted to fall within Region II is similar at all body sizes. This is true as a consequence of the specific relationships predicted by the constrained model outlined above; most deviations from the observed pattern would lead to differential scaling between observed and predicted tooth row dimensions.

Data on human muscle activity patterns during forceful biting (Spencer, 1998) (see above) also provide support for the constrained model that conflicts with the patterns of muscle position reported here. As predicted by the model, balancing side muscle activity declines relative to working side activity as the bite point is moved from M^1 to M^3 . However, such changes in muscle activity are unnecessary (and suboptimal) during maximum bite force production within Region I. Therefore, if the molar dentition does not usually lie within Region II, there should be no need for the observed reduction of balancing side muscle activity as the bite point moves posteriorly along the molars. Since humans resemble other anthropoid taxa in the relative positioning of

the adductor muscles and the relative effective length and position of Region II, there is no evidence to suggest that this pattern of muscle activity is unique to them.

A central question presents itself when trying to resolve the incongruity among these various observations: why does the estimated muscle resultant force lie more posteriorly than it is theoretically required to by the constraints on distractive joint reaction forces? In the following section, several compatible answers to this question are explored. These are related to alternative loading conditions, gape, and the introduction of a safety factor against distraction of the TMJ.

Alternative loading conditions

The method used in this study to estimate the position of the point where the muscle resultant force intersects the occlusal plane assumes the simple loading condition of static isometric biting near centric occlusion. However, this intersection point must change during different types of loading. If the avoidance of distractive joint reaction forces is potentially of selective importance during most types of loading, it is reasonable to expect the masticatory system to be configured so that such forces are not experienced during behaviors other than isometric bite force production. Two such behaviors may be particularly relevant.

First, Greaves (1978) modeled the muscle resultant force at a fixed anteroposterior position, the location of which is determined by the positions of the maximum magnitude force vectors for each homologous muscle group (i.e., the masseter, temporalis, and medial pterygoid muscles). During submaximum bite force production, however, a widening range of anteroposterior positions must be available since 1) the muscles intersect the occlusal plane at different A-P positions, 2) single muscles may, through heterogeneous activity, produce forces of variable position (Herring et al., 1979; Tonndorf et al., 1988; Blanksma et al., 1992), and 3) it has been shown both theoretically and experimentally that many combinations of muscle activity are adequate for the generation of a bite force with a given magnitude (Koolstra et al., 1988; van Eijden et al.,

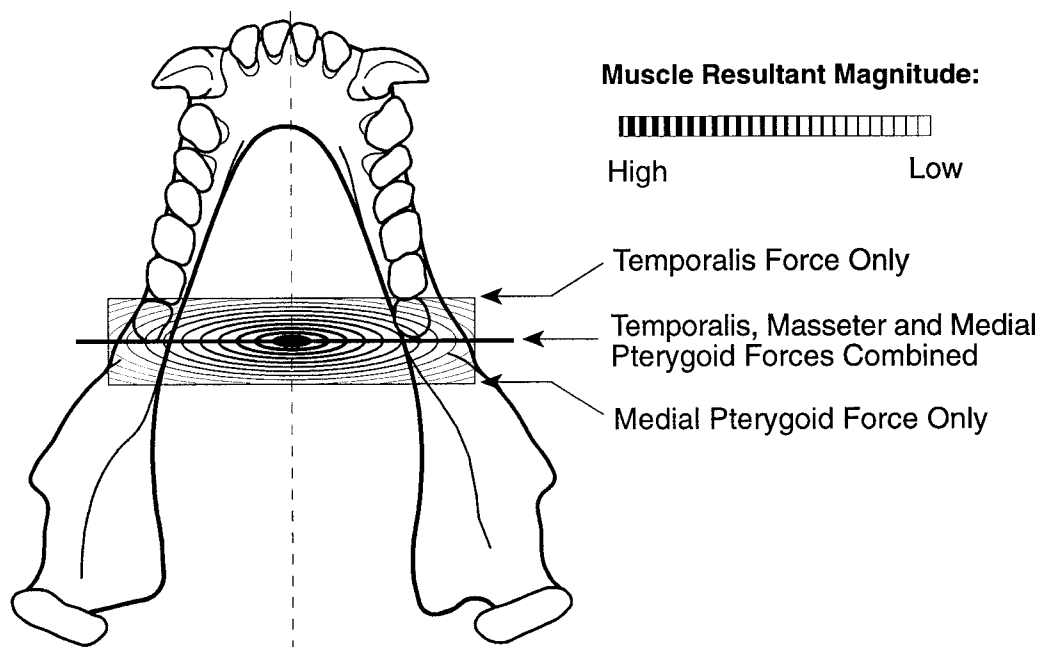


Fig. 8. Occlusal view of mandible showing the zone of potential muscle resultant force positions. Muscle resultant force magnitudes will be maximum at the center of this zone and will diminish with the distance from this position. With the muscle resultant force

positioned as assumed by Greaves (1978) (bold transverse line), more posterior molars will lie within this zone; biting on them may lead to tensile joint reaction forces during submaximum force production.

1988, 1990; van Eijden, 1991). Were the anterior temporalis muscle relatively more active than the masseter-medial pterygoid complex, for example, the muscle resultant force would lie more anteriorly relative to the position during maximum force production.

Rather than simply moving mediolaterally along a transverse line, therefore, a submaximum muscle resultant force can more realistically be modeled at any A-P location within a specific zone (Fig. 8). The size of this zone will increase as lower magnitude bite forces are required, and its ultimate size will be determined by the positions of the individual muscle groups; it cannot extend anterior to the force vector for the posterior temporalis or posterior to the medial pterygoid force. Any bite points lying within this zone could fall posterior to the muscle resultant force during submaximum bite force production, resulting in joint distraction. Of course, the muscle resultant force magnitude will be low near the bound-

aries of this region, and distractive joint forces are likely to be correspondingly weak. However, selection may favor a morphology in which the dentition lies anterior to some or all potential submaximum muscle resultant positions rather than just the transverse line where the muscle resultant force is maximum.

Mastication is a dominant type of loading for which these considerations may be relevant. Maximum magnitude bite forces are rarely produced during mastication (Hylander, 1979a), and the muscle resultant force can therefore move both mediolaterally and anteroposteriorly within the constraints of the model. Furthermore, the posterior temporalis muscle is active during mastication, both in the stabilization of the working side joint and during retraction of the balancing side mandibular condyle near the end of the power stroke (Ahlgren, 1966; Møller, 1966). The force of this muscle may be relatively high in magnitude, and it intersects the occlusal plane more anteriorly

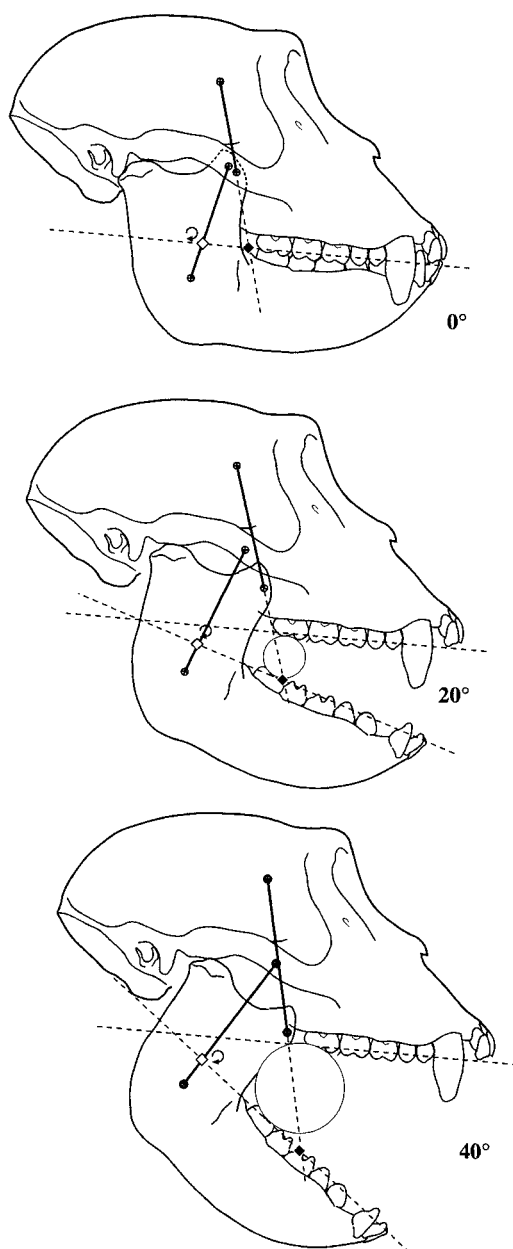


Fig. 9. Representation of the changes in muscle force vector orientation and position relative to the mandible at differing degrees of gape. As gape increases, the anterior temporalis force vector intersects the mandible much more anteriorly (\blacklozenge), while the masseter (and medial pterygoid not shown) vector will intersect slightly more posteriorly (\blacklozenge). These changes are based on an assumed center of rotation positioned at the circular arrow.

than any other muscle vector (due to its strong posterior inclination). It has the potential, therefore, to pull the muscle resultant force anteriorly. While it probably does not do so during maximum isometric biting (Pruim et al., 1978; van Eijden et al., 1988, 1990; van Eijden, 1990, 1991; Blanksma and van Eijden, 1990), this possibility may be realized during mastication. If the maximum magnitude muscle resultant force were positioned as assumed by Greaves (1978), this anterior migration of the resultant during mastication would increase the possibility that it would pass anterior to the bite force, resulting in tensile joint reaction forces. The more posterior position of the muscle resultant force estimated in this study may therefore be the result of selection against distraction of the TMJ during mastication or submaximum force production in general.

A second loading behavior that may influence the position of the muscle resultant vector is the application of loads on more distal teeth when the mandible is in an abducted position. The muscle vector/occlusal plane intersection points presented in Figure 7 were calculated under the assumption that the mandible is in centric occlusion. When applying force to a resistant food object, however, the mandible will be abducted to a greater or lesser degree depending on object size. Figure 9 illustrates the theoretical effects of changes in mandibular position on the relative positions of the muscle force vectors. Because the mandibular insertion point of the temporalis muscle probably lies well above the instantaneous center of rotation, it will move anteriorly (and inferiorly) as the mandible is abducted, while those for the masseter and medial pterygoid muscles move slightly posteriorly. The temporalis muscle vector will therefore intersect the mandible at a more anterior position at wider gapes. Given the large magnitude and more rapid rate of repositioning of the temporalis force vector, it is likely that the resultant muscle force vector migrates anteriorly as gape increases. Its chances of falling outside of the triangle of support will therefore be increased.

While very large objects are probably rarely processed on distal molars, high mag-

nitude forces could potentially be applied to these teeth at less abducted positions (less than 20°), either intentionally or by inadvertently biting on a resistant object. On these occasions, the degree of anterior migration of the muscle resultant suggested in Figure 9 could lead to joint distraction and possible injury. As with submaximum force production, this possibility could be expected to provide selection pressures favoring a conservative masticatory system configuration in which the muscle resultant is positioned more posteriorly than predicted by Greaves (1978). Both of these explanations rely on the premise that the TMJ should not be distracted.

Gape

An alternative hypothesis regarding the observed posterior location of the muscles of mastication in anthropoids derives from the need to produce adequate gape. The importance of abducting the mandible to some minimum gape during behaviors related to food processing or display has frequently been implicated as an important influence on masticatory muscle morphology in mammals (Herring, 1972, 1975; Herring and Herring, 1974; Emerson and Radinsky, 1980; Smith, 1984; Ravosa, 1991). One of the primary limits on gape is the length to which the adductor musculature can stretch. Proposed specializations of the masticatory system for producing wide gapes therefore include factors related to both internal muscle architecture (e.g., increased muscle fascicle length [Herring and Herring, 1974; Herring, 1975]) and aspects of muscle position and orientation. These latter may take the form of posterior migrations of the attachment areas of the masticatory adductor muscles; when attached closer to the axis of mandibular rotation, the muscles must stretch less for a given angle of gape.

Muscular and skeletal morphology consistent with predictions for specialized gape angles have been well documented in hippopotamids and tayassuids (Herring and Herring, 1974; Herring, 1975). Few such relationships have been found within primates (Smith, 1984; Ravosa, 1991). However, it is clear that the need for some minimum gape

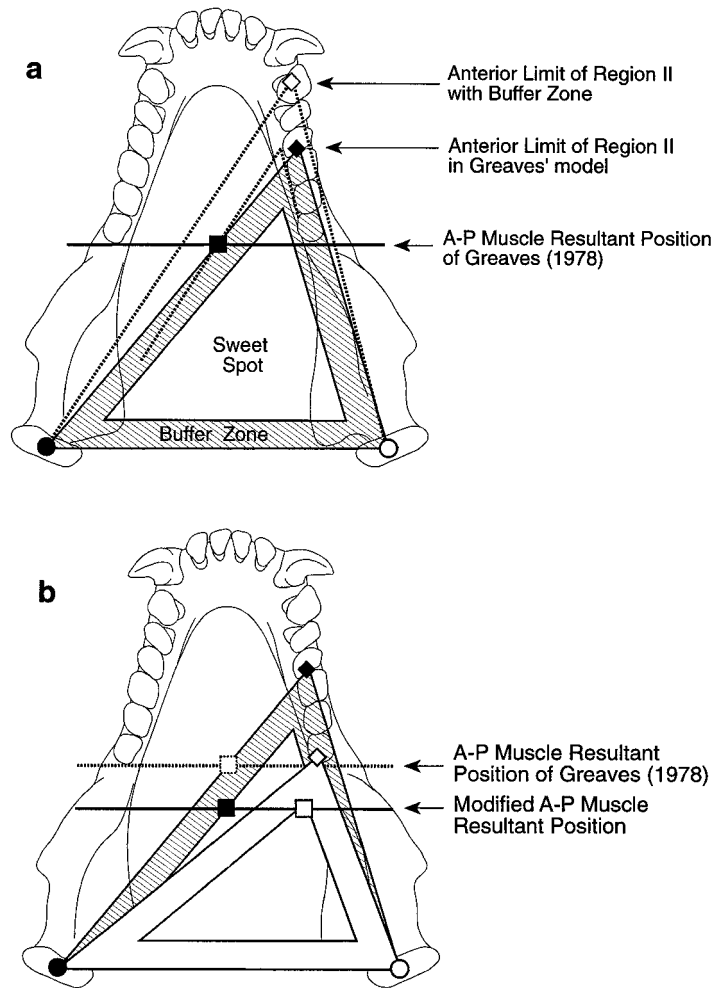
potential must be an important selective factor, even in animals not specialized for very wide gapes; all primates need to open their mouths to get food in. Furthermore, many open them wide for display purposes. The degree to which this alternative requirement has acted to constrain masticatory muscle position and morphology is difficult to estimate, but it must be included as an important potential influence on muscle position.

Safety factors

The hypotheses presented above may partially explain why the masticatory muscles are positioned so far posteriorly, and when considered together they make it unlikely that the muscle resultant could be positioned where Greaves (1978) assumed it to be. However, on their own they cannot reconcile the contradictory conclusions derived from the experimental and comparative morphological data summarized here. None of these hypotheses explains the observed reduction of balancing side muscle activity reported for humans (Spencer, 1998). These scenarios also fail to explain the observed correspondence between postcanine tooth row dimensions and the predictions of the modified constrained model.

There is an additional explanation, however, for the posterior location of the masticatory muscles that is consistent with these data. Greaves' (1978) constrained model predicts that during maximum bite force production within Region II the muscle resultant force will lie directly on the side of the triangle of support that connects the bite point and the balancing side joint reaction force. This position maximizes muscle resultant force magnitude by allowing the greatest balancing side muscle activity that does not lead to joint distraction. It therefore also results in zero magnitude working side joint reaction forces. Slight deviations from this position will either bring the muscle resultant into the triangle of support or (probably with equal likelihood) drop the muscle resultant outside of the triangle of support. Such deviations must be unavoidable during the dynamic process of loading even homogeneously textured foods and may be quite

Fig. 10. Occlusal view of mandible showing the effects on the distribution of Region II of requiring a buffer zone around the perimeter of the triangle of support. **a:** If no buffer zone exists, a muscle resultant force (■) positioned at the posterior end of the tooth row need not move toward the working side unless the bite point is positioned at or posterior to the closed diamond. However, if the muscle resultant force is required to lie well within the triangle of support (in the sweet spot), it will be forced toward the working side during biting at more anterior positions (at or posterior to the open diamond). **b:** Triangles of support for the most anterior (◆) and most posterior (◇) bite points in Region II, with their associated buffer zones. A muscle resultant force positioned as assumed by Greaves (1978) will lie within the buffer zone, while a more posteriorly positioned muscle resultant force will not. Due to the incorporation of a buffer zone, the predicted distribution of Region II is the same even when the muscle resultant force is positioned far posterior to the last molar.



large during the processing of less predictable objects. The optimal muscle resultant position assumed by Greaves (1978) may therefore be associated with relatively high frequencies of distractive joint loading.

The frequency with which the muscle resultant falls outside of the triangle of support can theoretically be reduced by positioning the resultant further within the triangle, in effect creating a buffer zone around the borders of the triangle of support and a "sweet spot" of more stable resultant positions within the triangle (Fig. 10a). The existence of such a buffer zone could provide an important safety factor and was briefly theorized by Greaves (1983:360): "For in-

creased stability of the jaw . . . it would be advantageous to have the muscle resultant lie well within the triangle of support rather than near the edge." However, Greaves did not recognize that the avoidance of a buffer zone changes our expectations regarding the interaction between muscle resultant position and Region II distribution.

Region II is defined as the area of potential bite points that will require a shift of the muscle resultant force toward the working side (to avoid tensile working side joint reaction forces). As shown in Figure 10a, however, avoidance of the buffer zone will require the muscle resultant to move toward the working side during biting at more

anterior bite points than predicted from Greaves' (1978) model. Furthermore, bite points positioned just anterior to the muscle resultant force (i.e., on the most distal molar in Greaves' model) will be associated with triangles of support whose buffer zone encloses the muscle resultant. The posterior end of Region II should therefore lie sufficiently anterior to the muscle resultant so that the resultant will not typically be positioned in the buffer zone. In this buffered model, therefore, the portion of the tooth row that will fall in Region II will be shifted anteriorly compared to the model proposed by Greaves (1978). Additionally, a gap will be present between Region II and the A-P position of the muscle resultant force.

Figure 10b shows how the predictions of Greaves' (1978) model regarding the position and length of Region II can be maintained with a modified, more posterior muscle resultant position if the proposed buffer zone and sweet spot exist. In this figure, Region II is distributed along the postcanine dentition as predicted based on a muscle resultant positioned at the posterior end of the tooth row. However, a more posteriorly positioned muscle resultant is used, and it is maintained within the sweet spot of the triangle of support at all bite point positions. Thus, the predictions of the buffered model regarding the length and distribution of Region II (and therefore the postcanine dentition) are similar to those of Greaves' (1978) constrained model, despite the conclusion that overall positional relationships within the masticatory system differ in the two models.

Implications for dietary adaptation

The data presented in this paper suggest that a constraint on distraction of the TMJ limits the evolution of the masticatory system in anthropoid primates. This constraint may also alter the adaptive response of the masticatory system to specific dietary selection pressures. Primates eat a wide variety of foods and experience a range of selection pressures related to generating masticatory forces. In the unconstrained lever model, predictions regarding the relative adaptive value of specific phenotypes derive from simple lever mechanics. For example, selec-

tion for efficient or high magnitude force production is expected to favor forms with a relatively high ratio of muscle force moment arm length to bite force moment arm length. This expectation holds for all bite point locations.

In some regards, the predictions of the constrained lever model (and the buffered version of this model proposed here) regarding dietary adaptation are similar to those of an unconstrained model. For biting on the anterior dentition (specifically in Region I), the predictions of the two models are the same since the constraint on joint distraction does not influence patterns of force production in this region. However, during postcanine biting this constraint limits the changes that may occur. For example, selection for high magnitude force production on the molars is commonly expected to lead to the anterior migration of the masticatory muscles and/or the posterior migration of the molars during evolution (Du Brul, 1977; Hylander, 1979a; Rak, 1983; Bouvier, 1986; Demes and Creel, 1988). However, either of these changes would alter the relative positions of the postcanine dentition and Regions I, II, and III. They are therefore expected to have additional mechanical consequences within the constrained model. In this example, the posterior portion of the tooth row would be forced into Region III, increasing the chances of distracting the TMJ. Furthermore, because the predicted maximum magnitude bite forces do not increase at more posterior bite points within Region II, changes in tooth position within this region may provide little or no advantage for high magnitude biting. Species experiencing selection for high magnitude postcanine force production are therefore not expected to exhibit changes in the relative anteroposterior positions of the muscles and teeth. Instead, the constrained model predicts that selection will favor more medially positioned tooth rows, a configurational change that allows more balancing side muscle force to be produced during forceful biting at points in Region II.

A diverse range of morphological patterns evident within anthropoid primates may stem from the selective trade-off between

increasing bite force magnitudes and avoiding joint distraction. For example, it has been proposed previously that a relatively high rate of third molar agenesis among Inuit is related to a configurational specialization for intensive incisor loading in this group (Spencer and Demes, 1993). In this case, a more posterior position for the dentition (relative to behaviorally unspecialized populations) and a relatively anterior position of the superficial masseter and anterior temporalis muscles have been attributed to selection for greater efficiency of force production at Region I bite points (Hylander, 1977; Spencer and Demes, 1993). These changes may have led to an increased frequency of joint distraction during distal molar biting. Third molar agenesis might then be an adaptive response related to minimizing this occurrence. Similar configurational and dental changes characterize other anthropoid groups that are behaviorally specialized for intensive force production on the incisors or canines, such as callitrichids, some pitheciines (*Cacajao* and *Chiropotes*), and *Cebus*. These groups each exhibit either relatively small third molar teeth or the evolutionary loss of their third molars. Furthermore, *Cacajao* and *Chiropotes* are characterized by molarized distal premolars (Rosenberger, 1979; Kay, 1990), an observation that is curious given their apparent reduction of molar occlusal area. These aspects of postcanine tooth form (and presumably function) are consistent with the altered position of the dentition relative to Region II brought about by selection for intensive incisor or canine loading.

CONCLUSIONS

The anthropoid primate masticatory system functions as a lever during the generation of masticatory forces. However, this simple model may be inadequate in attempting to explain many aspects of masticatory system diversity or function that are related to force production. For example, the data presented here indicate that the positional relationships among the muscles, joints, and postcanine dentition vary in finite and predictable ways across the full range of anthropoids. The consistency of this pattern sug-

gests that there has been some constant limiting influence on the configuration of the masticatory system during the evolution of this group. Such an influence is difficult to derive from the standard unconstrained lever model or from any presumed balance among variable and competing selection pressures.

The observed patterning within masticatory system diversity may be explained by Greaves's (1978) assumption that the TMJ should not be loaded by distractive forces. Greaves argued that the avoidance of such forces would be evident in changes in masticatory muscle activity along the tooth row and in a consistent positional interaction among the masticatory muscles, the joints, and the postcanine dentition. Data on human muscle activity support the first of these predictions (Spencer, 1998). The results of the current study support the second hypothesis. However, it is also apparent that the exact positional relationships predicted by Greaves are not realistic and that the constrained lever model must also be incomplete.

The observed discrepancy between morphological and experimental data suggests that selection favors the existence of safety factors that reduce the chances of joint distraction during diverse and dynamic loading situations. This buffered model of masticatory force production provides new expectations regarding the adaptive response of the primate masticatory system to dietary selection pressures. It may therefore help to explain a wide range of morphological patterns exhibited by living and extinct primates.

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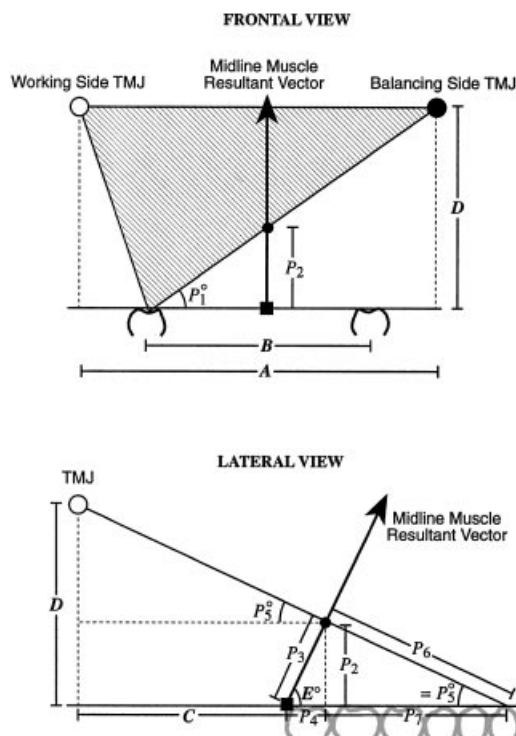


Fig. 11. Frontal and lateral views of relevant masticatory system components illustrating the five variables and derivative parameters used in the calculation of effective Region II length. The shaded zone visible in the frontal view is the triangle of support (viewed obliquely) for the most anterior bite point in Region II. The balancing side edge of the triangle intersects the midline muscle resultant force at the small closed circle. This triangle is seen edge-on in the lateral view as a diagonal line passing from the TMJ to the occlusal plane (horizontal line). A, biarticular breadth; B, palate breadth at M¹; C, anteroposterior distance from articular eminence (● or ○) to point of intersection of muscle resultant force and occlusal plane (■); D, height of articular eminence above occlusal plane; E, angle of muscle resultant force vector relative to occlusal plane (90° = perpendicular).

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APPENDIX

The five dimensions used in the calculation of effective Region II length are illustrated in Figure 11. The algorithm used for this calculation is as follows (refer to Fig. 11 for a diagram of the parameters that are

calculated at each step in this algorithm):

$$P_1^{\circ} = \left(\frac{D}{A - \left(\frac{A - B}{2} \right)} \right)$$

$$P_2 = \tan(P_1) * \left(\frac{B}{2} \right)$$

$$P_3 = \left(\frac{P_2}{\sin(E)} \right)$$

$$P_4 = \sqrt{P_3^2 - P_2^2}$$

$$P_5^{\circ} = \arctan \left(\frac{D - P_2}{P_4 + C} \right)$$

$$P_6 = \left(\frac{P_2}{\sin(P_5^{\circ})} \right)$$

$$P_7 = \sqrt{P_6^2 - P_2^2}$$

$$\text{Effective Region II Length} = P_7 + P_4.$$

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